FEEDING AND OXYGEN UPTAKE OF THE TROPICAL SEA URCHIN EUCIDARIS TRIBULOIDES (LAMARCK)[1,2]

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Feeding and oxygen uptake of echinoids have been studied by a number of investigators (for a recent review see Boolootian, 1966), but little work has been done on cidaroid urchins. These urchins are particularly interesting since they belong to an ancestral group from which all echinoids evolved (Durham and Melville, 1957).

There are over 150 living species and varieties in the family Cidaridae (Mortensen, 1928). Most of these live in the bathy-benthic zone, but some live in the littoral zone and a few live at great depths. In the West Indian region there are 12 species of cidaroids, one of which is littoral, the rest being found between 30 and 2000 meters (Mortensen, 1928). The littoral species, *Eucidaris tribuloides* (Lamarck), is relatively abundant in some habitats off southeastern Florida, particularly on coral reefs and rocky areas. It is easily maintained in aquaria where it grows at rates at least comparable with, and sometimes greater than those in the field (McPherson, in press). It is thus well-suited for laboratory studies.

This study was made to determine some of the factors which are important in the metabolism of *Eucidaris tribuloides.* Such parameters as temperature, season, size, and nutrition and their effect on oxygen uptake have been considered. Food preference and rate of feeding have been measured under laboratory conditions. This work will form a basis for studies on metabolism of deep-water cidaroids.

METHODS AND MATERIALS

Urchins used in respiration and feeding experiments were collected on Margot Fish Shoal, a "patch" coral reef several miles east of Elliot Key, Florida. After they were brought in from the field they were allowed to acclimate to aquarium conditions for at least several days before being used in experiments.

The food preference of *Eucidaris tribuloides* was tested for the boring sponge *Cliona lampa,* turtle grass (*Thalassia testudinum*), several algae (including *Dictyota* sp., *Liagona* sp.), and fish strips (mullet, *Mugil cephalus*). Eight rocks were arranged in a circle within a clean holding tank. The rocks were placed so that each was separated from the next by about 10 to 15 cm. The diameter of the circle of rocks was approximately one meter. Four of these rocks were infested with the boring sponge *Cliona lampa* or were placed on the other foods to be tested. Alternating with these were four rocks of similar size, but without any evident algal or

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animal growth. Sea water flowed into the tank, circulated around the tank and flowed out at a drain in the center of the circle of rocks. Urchins were placed in the center of the circle and the following day their positions were recorded in relation to the food. Those touching a non-food rock (control) were recorded as R. Those not touching any rock or food were recorded as 0. This was repeated on several days for each food with fresh urchins. The position of each rock was moved one place each day in the circle.

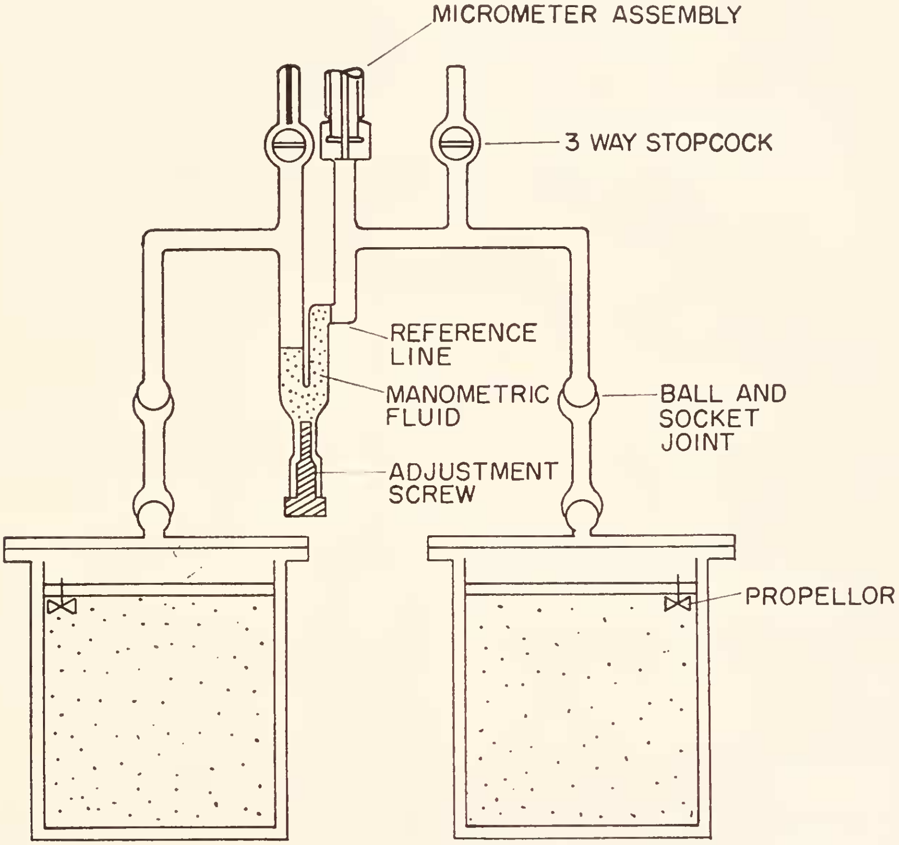

FIGURE 1. Schematic drawing of modified Scholander volumetric respirometer.

Before determining feeding rates urchins were maintained in aquaria two to three months and were offered an excess of rock infested with *Cliona lampa*. Feeding rate was determined in the laboratory on these individuals held in 950-cc. polyethylene cages. Weighed portions of rock infested with *Cliona lampa* were put into the cages and at the end of eight days the rock was reweighed (wet) and the amount eaten determined by differences between first and second weighings. Controls indicated that weight loss of rock during the experimental periods was not significant. Flow of sea water into aquaria was maintained in all feeding experiments at about two liters per minute.

Oxygen consumption was measured with a modified Scholander volumetric respirometer (Fig. 1). This consisted of a differential syringe manometer modified for attachment to two glass vessels (manometer obtained from RGI Inc., Vineland, New Jersey). The micrometer syringe had a total capacity of 200 microliters in 0.2 microliter divisions. The manometer was attached to the vessels by ground glass ball and socket joints. Vaseline was used as a lubricant for the joints and for the ground glass top and lip of the vessels. Hexanol with rodamine B dye was used as the manometer fluid.

The vessels contained a plastic ring with a magnetic stirrer. During respiration experiments small motors outside the vessels were used to stir and aerate the water. Water movement appeared to be an important factor for the well-being of urchins (Moore and McPherson, 1965).

The total volume of a vessel and its connecting tube was about 955 cc. The plastic ring had a volume of 120 cc. The air volume was maintained at about 65 cc., so that there was about 770 cc. in the vessel for sea water and for the urchin. The volumes of the urchins used ranged from about 5 to 80 cc., leaving 765 to 690 cc. of sea water, respectively. One vessel contained the experimental animal while the other (control vessel) contained only sea water. Carbon dioxide released by the urchin would be absorbed in the sea water, and would not increase significantly in the gas phase.

The general procedure for a respiration experiment was as follows:

(1) Sea water was put in both vessels and well aerated at a constant temperature (in a controlled-temperature bath which held the temperature to ±0.01° C.) for several hours.

(2) An urchin was placed in one vessel.

(3) The magnetic stirring apparatus was placed in both vessels and the water levels adjusted.

(4) The vessels were closed and connected to the manometer and then immersed into the controlled-temperature bath, so that the major air spaces were submerged.

(5) The stop cocks were left open so that both vessels were connected to the atmosphere.

(6) The sea water in the vessels was stirred with the magnetic stirrers.

(7) After about 60 minutes the vessels were closed to the atmosphere and readings were made every five or ten minutes for 30 minutes. In a few cases readings were made over periods longer than 30 minutes. The standard error for the mean oxygen uptake in cc. per hour per gm. dry weight, determined from 27 readings on six urchins at 20° C., was ±0.03.

(8) Determinations of oxygen uptake were made during the day, between the hours of 0900 and 1400.

After respiration and feeding rate experiments the test diameter of each urchin was measured. A few of these urchins were saved for later tests, but most were examined to determine sexual condition, gut content, and tissue weight. Sex and the presence or absence of ripe sex cells were determined by microscopic examinations of gonadal smears. Gonads of each individual were removed, measured volumetrically in a graduated cylinder and dried in an oven. Gonad index was calculated from the gonadal volume and test volume following the method of McPherson (in press). In order to determine the total dry tissue weight, the remaining parts of the urchin, with the exception of the coelomic fluid, were decalcified with 20% formic acid. An ion exchange resin (WIN 3000) was added to facilitate the removal of calcium from the tissue, following a method used for decalcification of teeth at the University of Miami Medical School. A test indicated that the dry weight of the coelomic fluid was negligible (less than 1% of the total weight of the somatic tissue). Tissue of the urchin was dried for 24 hours at 105° C.

The ash-free dry weight of both the urchin and its food, rock infested with *Cliona lampa,* was measured in several cases. The rock was weighed and decalcified by the same method described above for *Eucidaris tribuloides.* The decalcified and dried residue of either of these was burned in a muffle furnace at 500° C. for 24 hours, and then reweighed. The difference between the dry weight before and after burning was used as an estimate of the ash-free dry tissue.

RESULTS

1. *Food preference*

In a starved state *Eucidaris tribuloides* would consume practically anything including wooden and even fiber-glassed sides of holding tanks. Under normal feeding conditions, however, these urchins showed a preference for the sponge *Cliona lampa* (rock) over *Thalassia testudinum,* algal-covered rocks, and strips of fish (mullet) (Table I). Sixty-six per cent of those urchins tested were associated with the *C. lampa* as compared with 24% not associated with this food. In other tests 26% were associated with *T. testudinum* compared with 74% not associated with food; 26% were associated with algal covered rocks compared with 74% not associated with food; and 32% were associated with fish strips compared with 68% not associated with food. Because of this preference in the laboratory and because

TABLE I

Food preference of Eucidaris tribuloides in the laboratory with the foods: Cliona lampa rock (C), Thalassia testudinum (T), algal rock (A), and fish strips (F). R = clean rock; O = urchins not in contact with any of the above items. Chi square $(\chi)^2$ used to test significance of differences between the number of urchins associated with a food (rock) and those associated with a clean rock (control)

Total number tested	Percentages			χ^2
	C	R	O	
169	66	15	19	32.4
	T	R	0	
145	26	28	47	0.1
	A	R	0	
57	26	18	56	1.4
	F	R	0	
65	32	43	25	1.1

hard material was an important constituent of the gut content of urchins from the field, rock infested with *Cliona lampa* was selected as the food to be used in feeding rate and oxygen uptake experiments.

2. *Feeding rate*

Figure 2 gives the weight in gm. of wet rock (*Cliona lampa*) ingested per day for well-fed urchins during the period 1 to 9 February 1966. Urchins feed primarily on the surface of rock infested with *Cliona lampa,* ingesting both rock and sponge. Since the sponge tissue is concentrated at the surface and decreases with depth into the rock (Neumann, 1966), the urchins obtain relatively large amounts of tissue for the rock consumed. When the ash-free dry weight of the urchin and the rock consumed were determined, the intake corresponded roughly to 5% of the ash-free dry weight of the urchin per day.

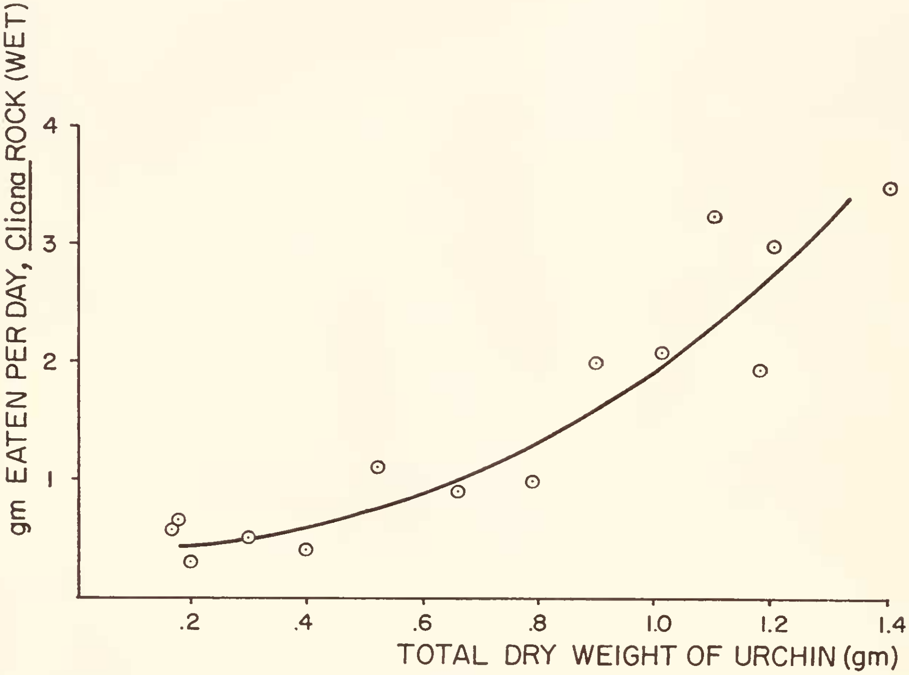

FIGURE 2. Feeding rate of well-fed individuals of *Eucidaris tribuloides* on rock infested with the boring sponge *Cliona lampa*. Experiment was made in aquaria during winter. Mean temperature 17° C. Line fitted by inspection.

3. *Preliminary experiments on oxygen uptake*

Tests were run to determine if changes in oxygen partial pressure or metabolic products would significantly change the rate of oxygen uptake of *Eucidaris tribuloides*. This was done by measuring oxygen consumption over periods of time considerably longer than normal respiration experiments. If changes in either of these factors significantly affected respiration during the normal tests then their effects should have been even more obvious in longer tests. The actual decrease in oxygen dissolved in the sea water that occurred during a test was measured in two cases. The micro-Winkler method described by Slack (1965) was used to measure the dissolved oxygen.

Urchins held in respirometers for varying periods of time over two hours showed some slight variation in oxygen consumption, but there appeared to be no significant trends in these tests. This was taken as an indication that any changes in the concentration of oxygen, carbon dioxide, metabolites or waste products in the respirometer water during these periods did not result in a measurable effect on the respiration of the urchin.

There was a 6% decrease in the dissolved oxygen in the respirometer water during an hour as indicated by micro-Winkler measurements. This small decrease in the dissolved oxygen in the respirometer water in spite of the oxygen consumed by the urchin is explained by the fact that there is a large source of oxygen in the respirometer vessel (compared with that used by the urchin). As the oxygen in the water is removed by the urchin it is replaced rapidly by oxygen in the air over the water due to the action of the magnetic stirrer. As stated, the volume of air over the water in the respirometer was about 65 cc. Since air contains about 200 cc. of oxygen per liter, each vessel before a run would contain about 13 cc. of oxygen in the air and about 5 cc. of oxygen dissolved in the water, depending on the temperature. If an average urchin removed 0.5 cc. of oxygen per hour, the loss at the end of two hours would be 1.0 cc. or only about 6% decrease in the total oxygen. This value is very close to the observed decreases.

TABLE II

O_2 consumption of Eucidaris tribuloides (well-fed and starved individuals). Urchins fed Cliona lampa rock. Temperature 30° C.

T.D. (mm.)	Well-fed	cc. O_2 per hour				
		Days of starvation				
		1	2	3	4	5
42	1.23	1.00	0.96		0.98	
26	0.46	0.34	0.34			
20	0.23	0.20				
28	0.65	0.65		0.28		
36	0.86	0.61		0.59		0.60
30	0.74	0.57	0.58			0.55

4. Oxygen uptake and nutrition

The effect of nutrition on oxygen consumption was studied by comparing the respiration of well-fed and starved urchins. Well-fed urchins were defined as those which were exposed to the food *Cliona lampa* and had this material in their gut. Starved urchins were defined as those which had been offered *Cliona lampa* in the laboratory, and which were then removed from this food for varying periods of time and held in clean polyethylene cages.

Respiration was measured individually on six well-fed urchins. These urchins were starved, and on one or more successive days their oxygen consumption was

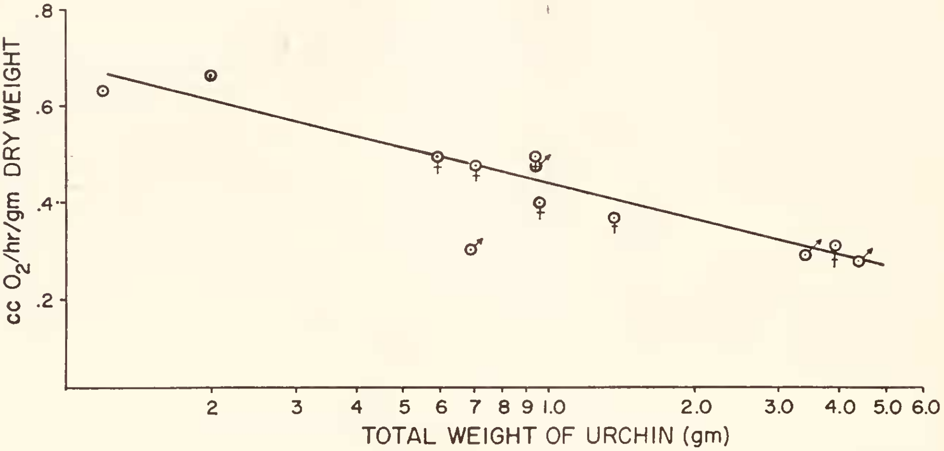

FIGURE 3. Relative oxygen uptake of *Eucidaris tribuloides*. Experiment was made in winter at 20° C.

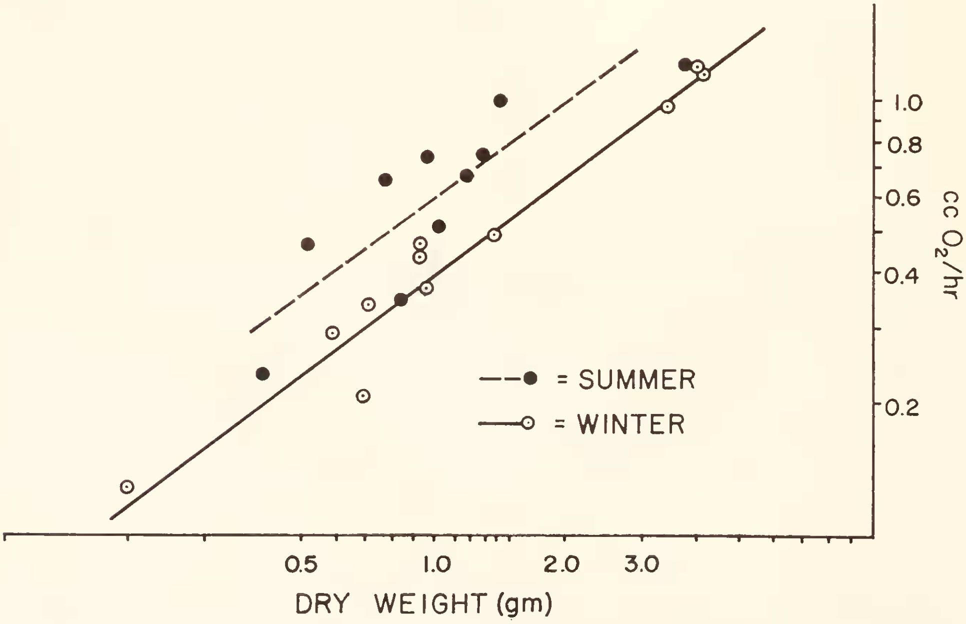

FIGURE 4. Oxygen uptake of *Eucidaris tribuloides* plotted against body size during summer at 30° C. (b = 0.65) and during winter at 20° C. (b = 0.70). Urchins well-fed.

remeasured. This test indicated that oxygen uptake decreased markedly during the first day of starvation, but showed little change over the next few days (Table II). The mean oxygen uptake decreased 22% from the original rate during the first day. Since oxygen uptake was relatively stable during at least the first one to five days of starvation, this interval of time was selected as a standard starvation period for further work.

5. Oxygen uptake and reproduction

Gonadal condition and sex were determined for most of the urchins in which oxygen consumption was measured. There was no indication that these factors significantly affected respiration. In addition there was no significant correlation between relative oxygen uptake and gonad index.

6. Oxygen uptake and size

Relative oxygen consumption plotted against body weight showed the expected trend of decreasing oxygen uptake with increasing body size (Fig. 3). The smallest urchins tested respired about twice as fast as did the largest urchins, the latter being about 30 times as large as the former.

The relationship between metabolic rate and body size may be expressed in the formula (Bertalanffy, 1957):

$M = a\ W^b$, where M = cc. O_2 per hour consumed by the urchin
W = weight of urchin
b = log-log slope of the line which relates O_2 uptake to weight
a = the point at which the above line intercepts the ordinate M.

Figure 4 gives the oxygen consumption of *Eucidaris tribuloides* plotted against size at 20° and 30° C. (winter and summer). The slopes of the resulting lines are 0.70 (winter, 20° C.) and 0.65 (summer, 30° C.). These values indicate an oxygen uptake which is almost proportional to surface area (or $\frac{2}{3}$ power of weight). In some echinoderms "b" has been shown to decrease with increasing temperature, indicating that larger animals consume proportionally less oxygen than smaller animals as the temperature increases (Farmanfarmaian, 1966). This may be related to decreased ambient oxygen or increased oxygen demand but insufficient supply.

7. O_2 uptake and temperature

Two aspects of the effect of temperature on respiration were considered. First, the short-term effect of temperature change on oxygen consumption was measured for some individuals in order to determine the time required for respiration to reach a relatively stable rate. Urchins were taken from water with an ambient temperature of 28–29° C. and placed in respirometers at temperatures of 10°, 15° 20°, and 30° C. The oxygen uptake of urchins placed in water which was cooler than ambient fluctuated during the first 40 minutes, and after this remained relatively stable (Fig. 5). Oxygen uptake was low during the first 10 minutes, then rose to a maximum in 20 to 30 minutes, and then decreased to an intermediate value after about 40 minutes. The oxygen uptake of urchins tested at temperature near ambient showed little change in respiratory rate over the same interval (Fig. 5). Second, the effect of temperature on the stabilized rate of oxygen consumption was measured at the following temperatures: 10°, 11°, 15°, 20°, 24°, 26°, and 30° C. Urchins were placed in the respirometers at these controlled temperatures and allowed to acclimate for one hour, after which oxygen determinations were made. The urchins used in these tests were within the size range 28 to 35 mm. After each test the dry weight of the urchin was determined and the respiration was expressed as cc. oxygen per hour per gm. dry weight (Figs. 6 and 7). The mean

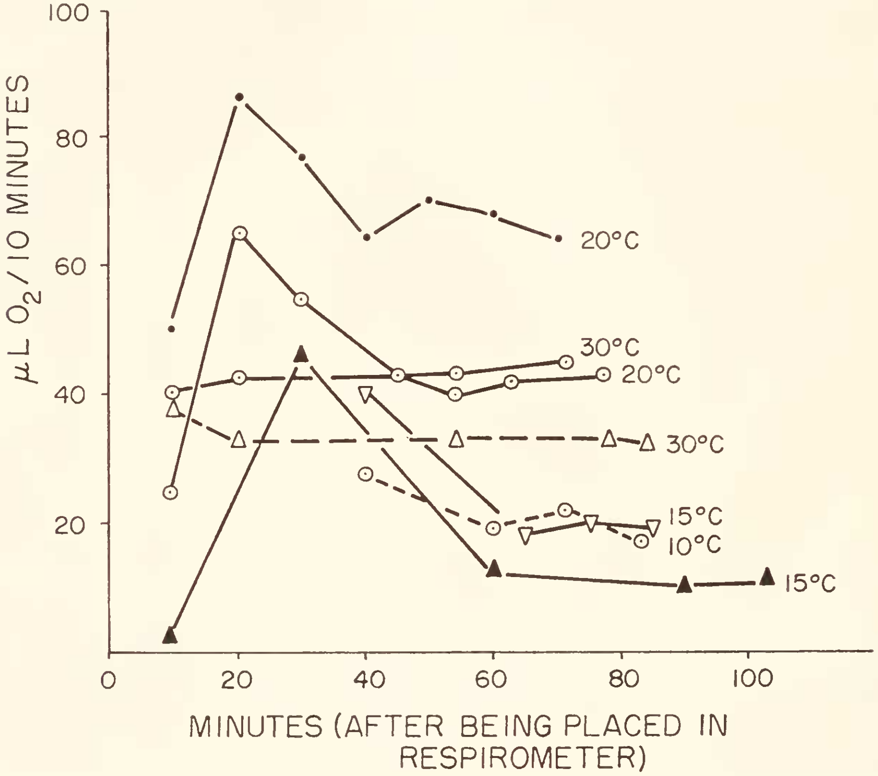

Figure 5. The immediate effect of temperature change on the oxygen uptake of *Eucidaris tribuloides*. Urchins were moved from ambient water with a temperature of 28–29° C. to water in the respirometer at different temperatures.

oxygen consumption for each temperature and the Q_{10} for each 5° C. interval between 10° and 30° C. were then calculated. Both starved and well-fed urchins were used (but these were considered separately).

The stabilized rate of oxygen consumption of *Eucidaris tribuloides* at different temperatures was measured in both summer and winter to determine if there were seasonal acclimation. The log of the mean oxygen consumption for each of the temperatures given above was plotted following the method given by Prosser and Brown (1961), and the degree of translation and rotation of the resulting curves for winter and summer was described (Figs. 6 and 7).

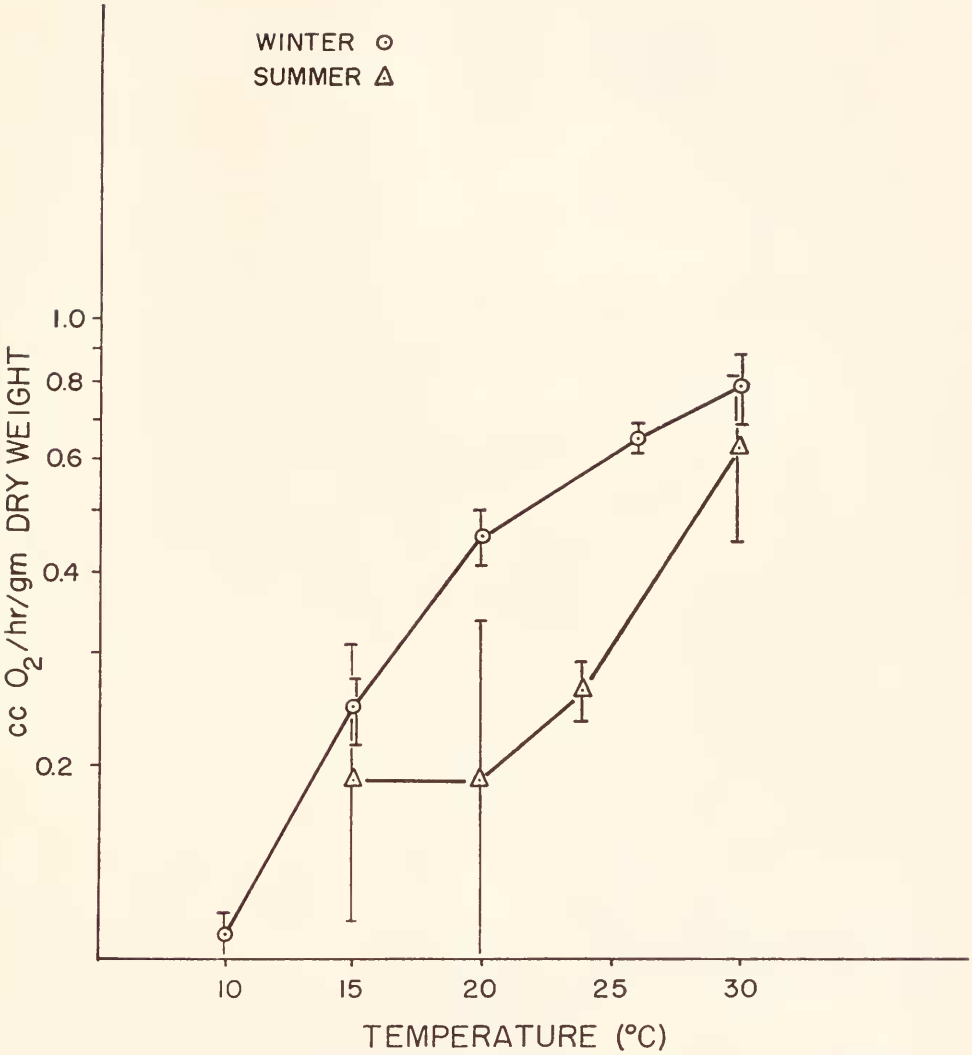

Figure 6. Mean oxygen uptake of individuals of *Eucidaris tribuloides* at stabilized rates for different temperatures. Urchins well-fed. The vertical lines give the 95% confidence intervals.

The Q_{10} of well-fed urchins increased rapidly in summer and decreased in winter as the temperature was increased from 15° to 30° C. The Q_{10} of starved urchins over a similar temperature range was more variable and manifested less overall change than that of the well fed individuals. In summer it increased 1.1 units in the temperature range 15° to 30° C. as compared with 3.4 units for the well-fed urchins. In winter it was essentially the same at high and low temperatures (Table III). These facts indicate that in both summer and winter well-fed

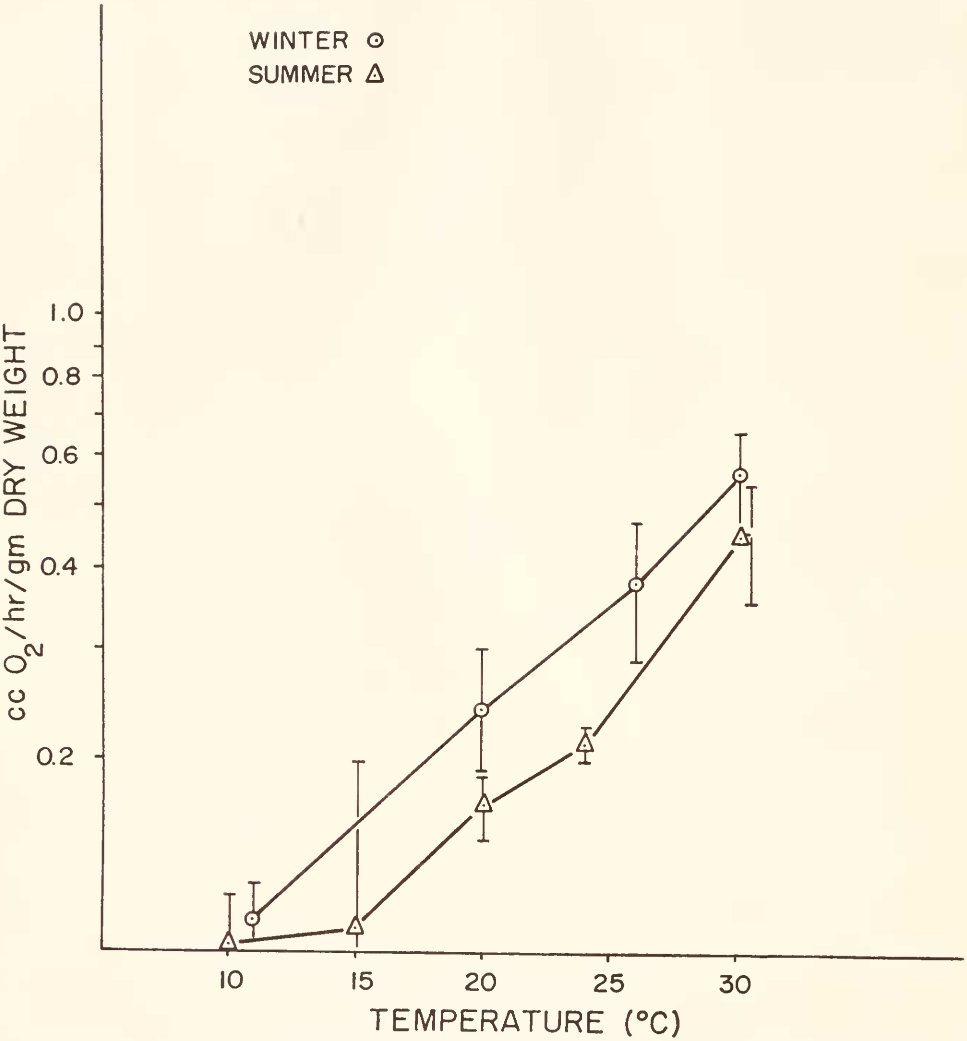

FIGURE 7. Mean oxygen uptake of individuals of *Eucidaris tribuloides* at stabilized rates for different temperatures. Urchins starved. The vertical lines give the 95% confidence intervals.

urchins were probably more sensitive to temperature changes in their stabilized respiratory rates than were starved urchins.

Both starved and well-fed urchins exhibited partial seasonal acclimation in which oxygen consumption curves were well above summer curves at the corresponding temperatures. The acclimation was not complete since the mean summer oxygen consumption was higher at the summer ambient than the mean winter oxygen consumption at the winter ambient. The difference between the mean summer and winter oxygen consumption curves of the starved urchins was less than that between the mean summer and winter curves of the well-fed urchins. This suggests that the process of feeding or digestion may play an important part in acclimation over normal environmental temperature ranges.

At 30° C., which is close to the summer ambient, the oxygen consumption curves tended to converge while at the winter ambient of 20° C. they were widely separated. This pattern resembled what Prosser and Brown (1961) have called translation and clockwise rotation (convergence at higher temperatures). At temperatures below the winter ambient there was a second convergence of oxygen consumption curves, so that around 10° C. there was little difference in the O_2 consumption of winter or summer urchins (no acclimation).

Table III

Q_{10} of well-fed and starved urchins (Eucidaris tribuloides) in winter and summer. Determined from changes in the mean oxygen uptake given in Figures 6 and 7

Well-fed		Starved	
Temperature, ° C.	Q_{10}	Temperature, ° C.	Q_{10}
Summer		Summer	
15–20	1.0	10–15	1.2
20–35	2.2	15–20	2.4
25–30	4.4	20–25	1.7
		25–30	3.5
Winter		Winter	
10–15	5.2	11–15	2.5
15–20	3.4	15–20	2.1
20–25	1.8	20–25	2.3
25–30	1.6	25–30	2.7

Discussion

Eucidaris tribuloides feeds on hard particles of limestone rock deriving nourishment from associated organisms (McPherson, in press). Since boring and encrusting sponges are prevalent on rocks in tropical seas these might well be important in the nutrition of this urchin. The preference of *E. tribuloides* in aquaria for the boring sponge *Cliona lampa* might be an indication of the importance of sponge in the diet of this species.

The relatively high rate of feeding observed in the laboratory indicates that *Eucidaris tribuloides* is a potential erosive agent. Urchins apparently fed throughout the year as indicated by the presence of food in individuals collected monthly in the field, and by observations of feeding in aquaria throughout the year (McPherson, in press). Urchins, of the mean size of those found on coral reefs, consumed about one to two gm. of wet carbonate rock per day in laboratory experiments. The feeding rate in the field, however, is probably less than that measured in the laboratory, as indicated by a slower growth rate in the former area than in the latter (McPherson, in press). Lewis (1964) stated that carbonate ingestion by *Diadema antillarum* may be of some importance in the process of erosion of certain zones of the coral reef. In this habitat he determined that *D. antillarum* ingested a mean weight of at least two gm. of carbonate per day. This intake in an area of high density, such as that reported by Randall *et al.* (1964) of 13.4 urchins per square meter off the Virgin Islands, would result in the removal of a considerable amount of coral rock. Erosion caused by *E. tribuloides,* however, would probably be much less than that caused by *D. antillarum* since the density and feeding rate of the former are probably much lower than that of the latter. McPherson (in press) reported a maximum mean density for *E. tribuloides* of two per square meter on French Reef, Florida. In other places off southeastern Florida densities were much less than that observed on this reef.

Under the experimental conditions used in this study food, size of organism, and temperature were important factors influencing the oxygen uptake of *Eucidaris tribuloides.* This is not surprising since these factors are all generally important in the metabolism of invertebrates (Zeuthen, 1947). It is interesting, however, that *E. tribuloides* does manifest some control over its oxygen uptake when temperature changes. Sudden changes in temperature resulted in a rather unstable rate of oxygen consumption, but this only lasted some minutes, and in an hour the rate of respiration became relatively stable. Slow changes in temperature, such as those which occur seasonally, had only a slight effect on respiration since the urchins partially acclimated during this time. Partial control of respiration would allow these animals to maintain some independence from environmental temperature.

Farmanfarmaian and Giese (1963) found that *Strongylocentrotus purpuratus* from ambient water of 14–19° acclimated to water at 5° C. The oxygen consumption curves were similar to those described for seasonal acclimation of *Eucidaris tribuloides* with the cold-acclimated urchins having rates above the warmer living individuals (translation). The two oxygen consumption curves, for acclimated and non-acclimated urchins, also tended to converge at higher temperatures (clockwise rotation) as did those of *E. tribuloides.* Boolootian and Cantor (1965) reported that *Arbacia punctulata* acclimated to low temperatures did not have a higher O_2 consumption than urchins maintained at higher temperatures. They stated that this suggested that *Arbacia* and *Strongylocentrotus* have different physiological mechanisms for thermal acclimation.

There was little variation in oxygen uptake between individuals of *Eucidaris tribuloides* at temperatures well below their winter ambient (10° and 15° C.). Even urchins tested in different seasons and in different nutritional conditions had roughly the same oxygen consumption for that particular temperature used in the experiment. Processes involved in nutrition and acclimation presumably had ceased or decreased to such low levels that their effect on respiration was negligible.

Summary

1. In the laboratory *Eucidaris tribuloides* showed a food preference for rock infested with the boring sponge *Cliona lampa* over turtle grass (*Thalassia testudinum*), several algae, and fish strips.

2. In the laboratory, urchins consumed wet rock infested with *Cliona lampa* at rates ranging from less than one to over three gm. per day depending on the size of the urchin.

3. Oxygen consumption of urchins was measured in the laboratory with a modified Scholander volumetric respirometer.

4. Oxygen uptake decreased significantly during the first day of starvation, but then remained relatively stable during several successive days of starvation.

5. There was not a significant correlation between gonad index or sex of the urchin and relative oxygen uptake.

6. Relative oxygen consumption decreased with increasing size of the urchin. Values for "b" indicated an oxygen uptake which was almost proportional to surface area at 20° and 30° C.

7. Oxygen uptake fluctuated during the first hour when urchins were placed in water several degrees colder than their ambient water. At the end of this hour, however, the rate of oxygen uptake had become relatively stable. Well-fed urchins manifested greater changes in their stabilized rates of oxygen uptake (Q_{10}) at different temperatures than did starved urchins.

8. Urchins manifested partial seasonal acclimation of oxygen uptake as indicated by the fact that winter oxygen consumption curves were well above summer curves at the corresponding temperatures. The acclimation was probably not complete since mean summer oxygen uptake was higher at the summer ambient than the mean winter oxygen uptake at the winter ambient.

LITERATURE CITED

Bertalanffy, L. von. 1957. Quantitative laws in metabolism and growth. *Quart. Rev. Biol.*, **32**: 217–231.

Boolootian, R. A., Ed., 1966. Physiology of Echinodermata. John Wiley and Sons, New York, 822 pp.

Boolootian, R. A., and H. Cantor, 1965. Preliminary report on respiration, nutrition and behavior of *Arbacia punctulata*. *Life Sci.*, **4**: 1567–1571.

Cerame-Vivas, M. J., and I. E. Gray, 1966. The distributional pattern of benthic invertebrates of the continental shelf off North Carolina. *Ecology*, **47**: 260–270.

Durham, J. W., and R. V. Melville, 1957. A classification of echinoids. *J. Paleont.*, **31**: 242–272.

Farmanfarmaian, A., 1966. The respiratory physiology of echinoderms. pp. 245–265. *In:* R. A. Boolootian (ed.) Physiology of Echinodermata. John Wiley and Sons, New York, 822 pp.

Farmanfarmaian, A., and A. C. Giese, 1963. Thermal tolerance and acclimation in the western purple sea urchin, *Strongylocentrotus purpuratus*. *Physiol. Zoöl.*, **36**: 237–243.

Lewis, J. B., 1964. Feeding and digestion in the tropical sea urchin *Diadema antillarum* Philippi. *Canad. J. Zool.*, **42**: 549–557.

McPherson, B. F., In press. Contributions to the biology of the sea urchin *Eucidaris tribuloides* (Lamarck). *Bull. Mar. Sci.*

Moore, H. B., and B. F. McPherson, 1965. A contribution to the study of the productivity of the urchins *Tripneustes esculentus* and *Lytechinus variegatus*. *Bull. Mar. Sci.*, **15**: 855–871.

Mortensen, T., 1928. A Monograph of the Echinoidea. *1*, C. A. Reitzel, Copenhagen, 551 pp.

Neumann, C. A., 1966. Observations on coastal erosion in Bermuda and measurements of the boring rate of the sponge *Cliona lampa*. *Limnol. Oceanogr.*, **11**: 92–108.

Prosser, C. L., and F. A. Brown, Jr., 1961. Comparative Animal Physiology, second edition, W. B. Saunders, Philadelphia, 688 pp.

Randall, J. E., R. E. Schroeder and W. A. Starck, 1964. Notes on the biology of the echinoid *Diadema antillarum*. *Caribb. J. Sci.*, **4**: 421–433.

Slack, K. V., 1965. A micro kit for dissolved oxygen determination. Water resources division bulletin, *U. S. Geol. Survey*; 16–18.

Zeuthen, E., 1947. Body size and metabolic rate in the animal kingdom. H. Hagerup, Copenhagen: 17–165.